Chapter 4

Photosynthesis

4.1 Lesson 4.1: Energy for Life: An Overview of Photosynthesis

Lesson Objectives

- Identify the kind of energy which powers life.
- Contrast the behavior of energy to that of materials in living systems.
- Analyze the way in which autotrophs obtain energy and evaluate the importance of autotrophs to energy for all life.
- Explain the relationship between autotrophs and heterotrophs.
- Discuss the importance of glucose to all life on earth.
- Compare the energy-carrying role of ATP to that of glucose.
- Explain the roles of chlorophyll and NADPH as sources of energy for life.
- Summarize the process of photosynthesis and write out the overall chemical equation for photosynthesis.
- Identify reactants, necessary conditions, and products in the chemical equation for photosynthesis.
- Describe the roles of chlorophyll and chloroplasts in photosynthesis.
- Identify the groups of organisms which are capable of photosynthesis.
- Discuss the many reasons photosynthesis is important to humans.

Introduction

All living things require an ongoing source of energy to do the work of life. You often see energy in action on a large scale: a whale breaches, apple blossoms swell and burst, a firefly glows, or an inky cap mushrooms overnight. However, energy works constantly to maintain life on a very small scale as well. Inside each cell of every organism, energy assembles chains of information and constructs cellular architecture. It moves tiny charged particles and giant protein molecules. Moreover, it builds and powers cell systems for awareness, response, and reproduction. All life's work requires energy.

Physics tells us that organized systems, such as living organisms, tend to disorder without a constant input of energy. You have direct, everyday experience with this law of nature: after a week of living in your room, you must spend energy in order to return it to its previous, ordered state. Tides and rain erode your sandcastles, so you must work to rebuild them. And your body, after a long hike or big game, must have more fuel to keep going. Living things show amazing complexity and intricate beauty, but if their source of energy fails, they suffer injury, illness, and eventually death.

Physics also tells us that, although energy can be captured or transformed, it inevitably degrades, becoming heat, a less useful form of energy. This is why organisms require a constant input of energy; the work they must do uses up the energy they take in. Energy, unlike materials, cannot be recycled. The story of life is a story of energy flow – its capture, transformation, use for work, and loss as heat.

Energy, the ability to do work, can take many forms: heat, nuclear, electrical, magnetic, light, and chemical energy. Life runs on **chemical energy** - the energy stored in covalent bonds between atoms in a molecule. Where do organisms get their chemical energy? That depends…

How Do Organisms Get Energy? Autotrophs vs. Heterotrophs

Living organisms obtain chemical energy in one of two ways.

Autotrophs, shown in **Figure** 4.1, store chemical energy in carbohydrate food molecules they build themselves. **Food** is chemical energy stored in organic molecules. Food provides both the energy to do work and the carbon to build bodies. Because most autotrophs transform sunlight to make food, we call the process they use **photosynthesis**. Only three groups of organisms - plants, algae, and some bacteria - are capable of this life-giving energy transformation. Autotrophs make food for their own use, but they make enough to support other life as well. Almost all other organisms depend absolutely on these three groups for the food they produce. The **producers**, as autotrophs are also known, begin **food chains** which feed all life. Food chains will be discussed in the *Principles of Ecology* chapter.

Heterotrophs cannot make their own food, so they must eat or absorb it. For this reason, heterotrophs are also known as **consumers**. Consumers include all animals and fungi and many protists and bacteria. They may consume autotrophs, or other heterotrophs or **organic molecules** from other organisms. Heterotrophs show great diversity and may appear far more fascinating than producers. But heterotrophs are limited by our utter dependence on those autotrophs which originally made our food. If plants, algae, and autotrophic bacteria vanished from earth, animals, fungi, and other heterotrophs would soon disappear as well. All life requires a constant input of energy. Only autotrophs can transform that ultimate, solar source into the chemical energy in food which powers life, as shown in **Figure** 4.2.

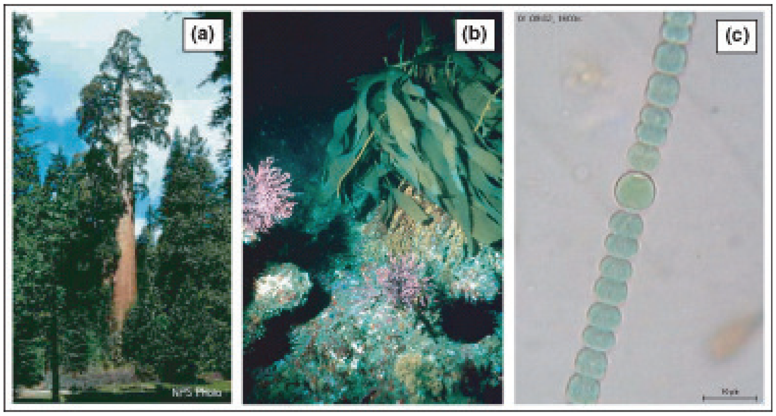


Figure 4.1: Photosynthetic autotrophs, which make food for more than 99% of the organisms on earth, include only three groups of organisms: plants such as the redwood tree (a), algae such as kelp (b), and certain bacteria like this *Anabaena* (c). (14)

Photosynthesis provides over 99 percent of the energy supply for life on earth. A much smaller group of autotrophs - mostly bacteria in dark or low-oxygen environments - produce food using the chemical energy stored in **inorganic molecules** such as hydrogen sulfide, ammonia, or methane. While photosynthesis transforms light energy to chemical energy, this alternate method of making food transfers chemical energy from inorganic to organic molecules. It is therefore called **chemosynthesis**, and is characteristic of the tubeworms shown in **Figure** 4.3. Some of the most recently discovered chemosynthetic bacteria inhabit deep ocean hot water vents or "black smokers." There, they use the energy in gases from the Earth's interior to produce food for a variety of unique heterotrophs: giant tube worms, blind shrimp, giant white crabs, and armored snails. Some scientists think that chemosynthesis may support life below the surface of Mars, Jupiter's moon, Europa, and other planets as well. Ecosystems based on chemosynthesis may seem rare and exotic, but they too illustrate the absolute dependence of heterotrophs on autotrophs for food.

Food and Other Energy-Carrying Molecules

You know that the fish you had for lunch contained protein molecules. But do you know that the atoms in that protein could easily have formed the color in a dragonfly's eye, the heart of a water flea, and the whiplike tail of a *Euglena* before they hit your plate as sleek fish muscle? As you learned above, food consists of organic (carbon-containing) molecules which store energy in the chemical bonds between their atoms. Organisms use the atoms of food molecules to build larger organic molecules including proteins, DNA, and fats and

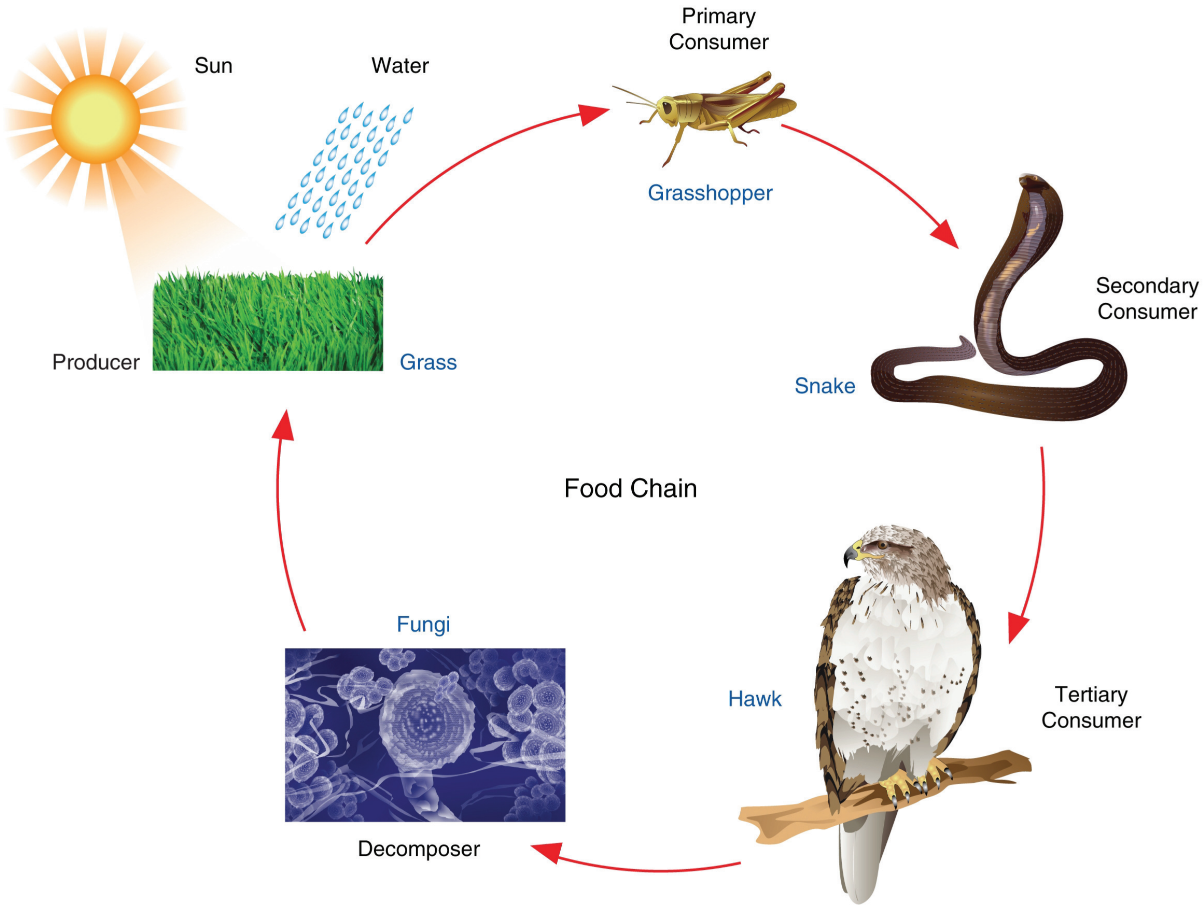


Figure 4.2: Food chains carry energy from producers (autotrophs) to consumers (heterotrophs). 99 percent of energy for life comes from the sun via photosynthesis. Note that only nutrients recycle. Energy must continue to flow into the system. (6)

Figure 4.3: Tubeworms deep in the Gulf of Mexico get their energy from chemosynthetic bacteria living within their tissues. No digestive systems needed! Photo: Charles Fisher (4)

use the energy in food to power life processes. By breaking the bonds in food molecules, cells release energy to build new compounds. Although some energy dissipates as heat at each energy transfer, much of it is stored in the newly made molecules. Chemical bonds in organic molecules are a reservoir of the energy used to make them. Fueled by the energy from food molecules, cells can combine and recombine the elements of life to form thousands of different molecules. Both the energy (despite some loss) and the materials (despite being reorganized) pass from producer to consumer – perhaps from algal tails, to water flea hearts, to dragonfly eye colors, to fish muscle, to you!

The process of photosynthesis, which usually begins the flow of energy through life, uses many different kinds of energy-carrying molecules to transform sunlight energy into chemical energy and build food.

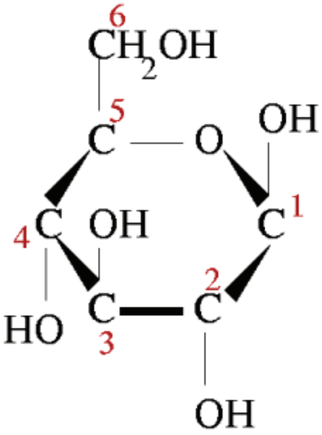
Some carrier molecules hold energy briefly, quickly shifting it like a hot potato to other molecules. This strategy allows energy to be released in small, controlled amounts. An example is **chlorophyll,** the green pigment present in most plants which helps convert solar energy to chemical energy. When a chlorophyll molecule absorbs light energy, electrons are excited and "jump" to a higher energy level. The excited electrons then bounce to a series of carrier molecules, losing a little energy at each step. Most of the "lost" energy powers some small cellular task, such as moving ions across a membrane or building up another molecule. Another short-term energy carrier important to photosynthesis, NADPH, holds chemical energy a bit longer but soon "spends" it to help to build sugar.

Two of the most important energy-carrying molecules are **glucose** and **ATP**, adenosine triphosphate. These are nearly universal fuels throughout the living world and both are also key players in photosynthesis, as shown below.

A molecule of glucose, which has the chemical formula $C_6H_{12}O_6$, carries a packet of chemical energy just the right size for transport and uptake by cells. In your body, glucose is the "deliverable" form of energy, carried in your blood through capillaries to each of your 100 trillion cells. Glucose is also the carbohydrate produced by photosynthesis, and as such is the near-universal food for life.

ATP molecules store smaller quantities of energy, but each releases just the right amount to actually do work within a cell. Muscle cell proteins, for example, pull each other with the energy released when bonds in ATP break open (discussed below). The process of photosynthesis also makes and uses ATP - for energy to build glucose! ATP, then, is the useable form of energy for your cells.

Glucose is the energy-rich product of photosynthesis, a universal food for life. It is also the primary form in which your bloodstream delivers energy to every cell in your body. The six carbons are numbered.



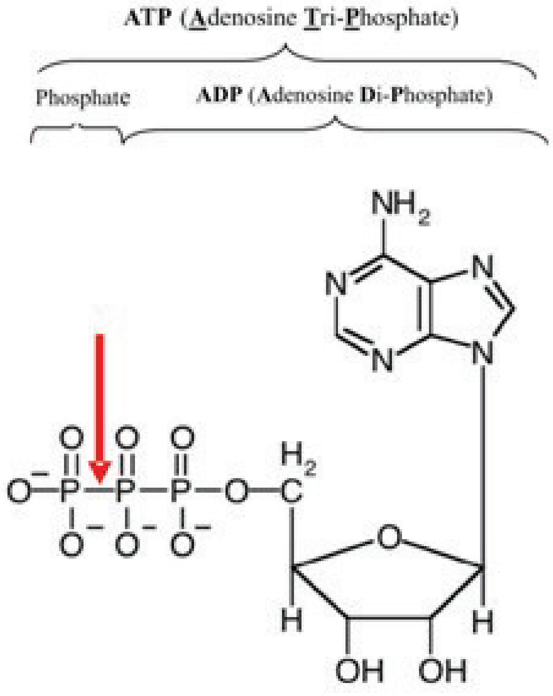
Why do we need both glucose and ATP? Why don't plants just make ATP and be done with it? If energy were money, ATP would be a quarter. Enough money to operate a parking meter or washing machine. Glucose would be a dollar bill (or $10) – much easier to carry around in your wallet, but too large to do the actual work of paying for parking or washing. Just as we find several denominations of money useful, organisms need several "denominations" of energy – a smaller quantity for work within cells, and a larger quantity for stable storage, transport, and delivery to cells.

Let's take a closer look at a molecule of ATP. Although it carries less energy than glucose, its structure is more complex. "A" in ATP refers to the majority of the molecule – adenosine – a combination of a nitrogenous base and a five-carbon sugar. "T" and "P" indicate the three phosphates, linked by bonds which hold the energy actually used by cells. Usually, only the outermost bond breaks to release or spend energy for cellular work.

An ATP molecule, shown below, is like a rechargeable battery: its energy can be used by the cell when it breaks apart into ADP (adenosine diphosphate) and phosphate, and then the "worn-out battery" ADP can be recharged using new energy to attach a new phosphate and rebuild ATP. The materials are recyclable, but recall that energy is not!

How much energy does it cost to do your body's work? A single cell uses about 10 million ATP molecules per second, and recycles all of its ATP molecules about every 20-30 seconds.

A red arrow shows the bond between two phosphate groups in an ATP molecule. When this bond breaks, its chemical energy can do cellular work. The resulting ADP molecule is recycled when new energy attaches another phosphate, rebuilding ATP.



Keep these energy-carrying molecules in mind as we look more carefully at the process which originally captures the energy to build them: photosynthesis. Recall that it provides nearly all of the food (energy and materials) for life. Actually, as you will see, we are indebted to photosynthesis for even more than just the energy and building blocks for life.

Photosynthesis: The Most Important Chemical Reaction for Life on Earth

What do pizza, campfires, dolphins, automobiles, and glaciers have in common? In the following section, you'll learn that all five rely on photosynthesis, some in more ways than one. Photosynthesis is often considered the most important chemical reaction for life on earth. Let's delve into how this process works and why we are so indebted to it.

Photosynthesis involves a complex series of chemical reactions, each of which convert one substance to another. These reactions taken as a whole can be summarized in a single symbolic representation – as shown in the chemical equation below.

$$6CO_2 + 6H_2O + \text{light} \xrightarrow{\substack{\text{Chloroplast}\\ \text{Chlorophyll}\\ \text{Enzymes}}} C_6H_{12}O_6 + 6O_2$$

We can substitute words for the chemical symbols. Then the equation appears as below.

$$\text{Carbon dioxide + water + light energy} \xrightarrow{\substack{\text{Chloroplast}\\ \text{Chlorophyll}\\ \text{Enzymes}}} \text{glucose + oxygen gas}$$

Like all chemical equations, this equation for photosynthesis shows reactants connected by plus signs on the left and products, also connected by plus signs, on the right. An arrow indicating the process or chemical change leads from the reactants to the products, and conditions necessary for the chemical reaction are written above the arrow. Note that the same kinds of atoms, and number of atoms, are found on both sides of the equation, but the kinds of compounds they form change.

You use chemical reactions every time you cook or bake. You add together ingredients (the reactants), place them in specific conditions (often heat), and enjoy the results (the products). A recipe for chocolate chip cookies written in chemical equation form is shown below.

$$\underbrace{\text{Butter + sugar + eggs + flour + chocolate chips}}_{\text{REACTANTS}} \underbrace{\xrightarrow{\substack{\text{375 F}\\ \text{8—10 minutes}}}}_{\text{NECESSARY CONDITIONS}} \underbrace{\text{chocolate chip cookies}}_{\text{PRODUCT}}$$

Compare this familiar recipe to photosynthesis below.

$$6CO_2 + 6H_2O + \text{light} \xrightarrow{\substack{\text{Chloroplast}\\ \text{Chlorophyll}\\ \text{Enzymes}}} C_6H_{12}O_6 + 6O_2$$

The equation shows that the "ingredients" for photosynthesis are carbon dioxide, water, and light energy. Plants, algae, and photosynthetic bacteria take in light from the sun, molecules of carbon dioxide from the air, and water molecules from their environment and combine these reactants to produce food (glucose).

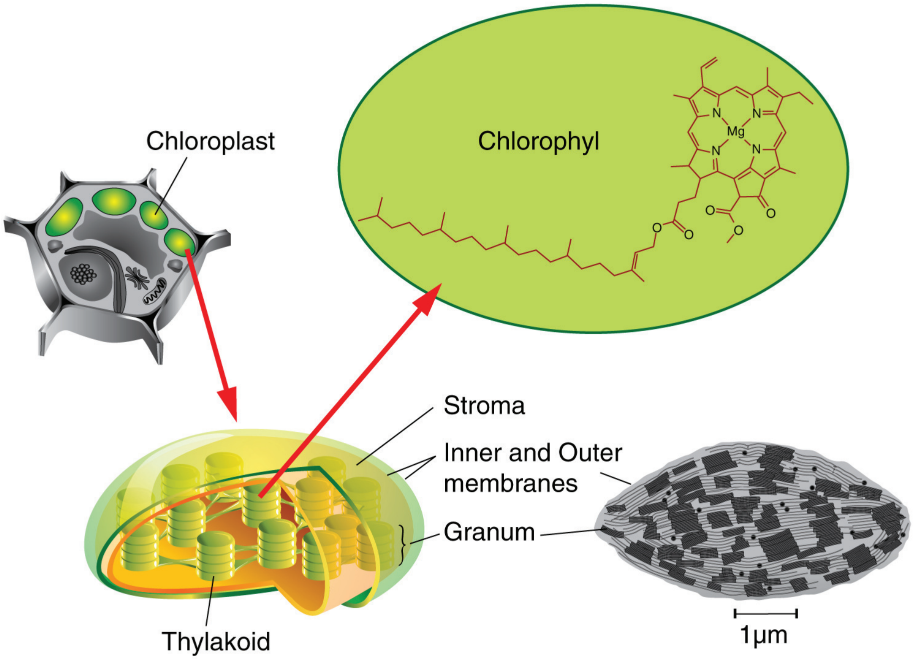
Of course, light, carbon dioxide, and water mix in the air even without plants. But they do not chemically change to make food without very specific necessary conditions which are found only in the cells of photosynthetic organisms. Necessary conditions include:

1. **enzymes** - proteins which speed up chemical reactions without the heat required for

cooking

2. **chlorophyll** - a pigment which absorbs light
3. **chloroplasts** - organelles whose membranes embed chlorophyll, accessory pigments, and enzymes in patterns which maximize photosynthesis

Within plant cells or algal cells, chloroplasts organize the enzymes, chlorophyll, and accessory pigment molecules necessary for photosynthesis.



When the reactants meet inside chloroplasts, or the very similar cells of blue-green bacteria, chemical reactions combine them to form two products: energy-rich glucose molecules and molecules of oxygen gas. Photosynthetic organisms store the glucose (usually as starch) and release the oxygen gas into the atmosphere as waste.

Let's review the chemical equation for photosynthesis once more, this time at the level of atoms as in the equation below.

$$6CO_2 + 6H_2O + \text{light} \xrightarrow[\text{Enzymes}]{\substack{\text{Chloroplast} \\ \text{Chlorophyll}}} C_6H_{12}O_6 + 6O_2$$

Look closely at its primary purpose: storing energy in the chemical bonds of food molecules. The source of energy for food is sunlight energy. The source of carbon atoms for the food molecules is carbon dioxide from the air, and the source of hydrogen atoms is water. Inside the cells of plants, algae, and photosynthetic bacteria, chlorophyll, and enzymes use the light energy to rearrange the atoms of the reactants to form the products, molecules of glucose and oxygen gas. Light energy is thus transformed into chemical energy, stored in the bonds which bind six atoms each of carbon and oxygen to twelve atoms of hydrogen – forming a molecule of glucose. This energy rich carbohydrate molecule becomes food for the plants, algae, and bacteria themselves as well as for the heterotrophs which feed on them.

One last detail: why do "6"s precede the CO_2, H_2O, and O_2? Look carefully, and you will see that this "balances" the equation: the numbers of each kind of atom on each side of the arrow are equal. Six molecules each of CO_2 and H_2O make 1 molecule of glucose and 6 molecules of oxygen gas.

Lesson Summary

All organisms require a constant input of **energy** to do the work of life.

- Energy cannot be recycled, so the story of life is a story of energy flow – its capture, transformation, use for work, and loss as heat.

Life runs on **chemical energy**.

- **Food** is chemical energy stored in organic molecules.
- Food provides both the energy to do life's work and the carbon to build life's bodies.
- The carbon cycles between organisms and the environment, but the energy is "spent" and must be replaced.

Organisms obtain chemical energy in one of two ways.

- **Autotrophs** make their own carbohydrate foods, transforming sunlight in **photosynthesis** or transferring chemical energy from inorganic molecules in **chemosynthesis**.
- **Heterotrophs** consume organic molecules originally made by autotrophs.
- All life depends absolutely upon autotrophs to make food molecules.

The process of **photosynthesis** produces more than 99% of all food for life, forming the foundation of most food chains.

- Only three groups of organisms – plants, algae, and some bacteria – carry out the process of photosynthesis.

All organisms use similar energy-carrying molecules for food and to carry out life processes.

- **Glucose** ($C_6H_{12}O_6$,) is a nearly universal fuel delivered to cells, and the primary product of photosynthesis.

- **ATP** molecules store smaller amounts of energy and are used within cells to do work.
- **Chlorophyll** and **NADPH** molecules hold energy temporarily during the process of photosynthesis.

The chemical equation below summarizes the many chemical reactions of photosynthesis.

$$6CO_2 + 6H_2O + \text{light} \xrightarrow[\text{Enzymes}]{\text{Chloroplast} \atop \text{Chlorophyll}} C_6H_{12}O_6 + 6O_2$$

- The equation states that the reactants (carbon dioxide, water and light), in the presence of chloroplasts, chlorophyll and enzymes, yield two products, glucose and oxygen gas.
- **Chlorophyll** is a pigment that absorbs sunlight energy.
- **Chloroplasts** are the organelles within plant and algal cells that organize enzymes and pigments so that the chemical reactions proceed efficiently.

In the process of photosynthesis, plants, algae, and blue green bacteria absorb sunlight energy and use it to change carbon dioxide and water into glucose and oxygen gas.

- Glucose contains stored chemical energy and provides **food** for the organisms that produce it and for many heterotrophs.
- Photosynthesized carbohydrates (represented here by glucose) make up the wood we burn and (over hundreds of millions of years) the coal, oil, and gas we now use as fossil fuels.
- Most of the oxygen gas is waste for the organisms which produce it.
- Both CO_2 consumed and O_2 produced affect the composition of earth's atmosphere; before photosynthesis evolved, oxygen was not part of the atmosphere.

Review Questions

1. Compare the behavior of energy to the behavior of matter in living systems.
2. Water and carbon dioxide molecules are reactants in the process of photosynthesis. Does this mean they are "food" for plants, algae, and blue-green bacteria? Use the definition of "food" to answer this question.
3. Compare autotrophs to heterotrophs, and describe the relationship between these two groups of organisms.
4. Name and describe the two types of food making found among autotrophs, and give an example of each. Which is quantitatively more important to life on earth?
5. Trace the flow of energy through a typical food chain (describing "what eats what"), including the original source of that energy and its ultimate form after use. Underline each form of energy or energy-storing molecule, and boldface each process which transfers or transforms energy.

6. Trace the pathway that carbon atoms take through a typical food chain, beginning with their inorganic source.
7. The fact that all organisms use similar energy-carrying molecules shows one aspect of the grand "Unity of Life." Name two universal energy-carrying molecules, and explain why most organisms need both carriers rather than just one.
8. A single cell uses about 10 million ATP molecules per second. Explain how cells use the energy and recycle the materials in ATP.
9. Discuss the importance of photosynthesis to humans in terms of food, fuel, and atmosphere. In what ways could you affect the process of photosynthesis to conserve these benefits?
10. Using symbols, write the overall chemical equation for photosynthesis, labeling the reactants, necessary conditions, and products. Then write two complete sentences which trace the flow of (1) energy and (2) atoms from reactants to products.

Further Reading / Supplemental Links

- Graham Kent, "Light Reactions in Photosynthesis" Animation. Bio 231 Cell Biology Lab, October 2004. Available on the Web at:
- `http://www.science.smith.edu/departments/Biology/Bio231/ltrxn.html.`
- Illustrator: Thomas Porostocky; Writer: Lee Billings; Map data adapted from MODIS observations by NASA's Terra and Aqua satellites; Graph data and reference: Biology, 4th ed., Neil A. Campbell, Benjamin/Cummings Publishing Company, 1996. "Crib Sheet #10, Photosynthesis." *Seed Magazine,* August 2007. Available on the Web at:
- `http://www.seedmagazine.com/news/uploads/cribsheet10.gif.`
- John Mynett, "Photosynthesis Animations." Biology4All, 01 January 2002. Available on the Web at:
- `http://www.biology4all.com/resources_library/details.asp?ResourceID=43`
- Kenneth R. Spring, Thomas J. Fellers, and Michael W. Davidson, "Introduction to Light and Energy." Molecular Expressions Optical Microscopy Primer. The Physics of Light and Energy, Last modified Aug 23, 2005. Available on the Web at
- `http://micro.magnet.fsu.edu/primer/lightandcolor/lightandenergyintro.html.`
- "Photosynthesis," "Electron Transport Chain" and "ATP Synthase" Animations. Virtual Cell Animation Collection, Molecular and Cellular Biology Learning Center, no date given. Available on the Web at:
- `http://vcell.ndsu.nodak.edu/animations/photosynthesis/index.htm.`

Vocabulary

ATP Adenosine triphosphate, the energy-carrying molecule used by cells to do work.

autotroph An organism capable of transforming one form of energy – usually light – into the food, or stored chemical energy, they need to do work.

chemosynthesis Process by which a type of autotroph makes food using chemical energy in inorganic molecules.

chlorophyll The primary pigment of photosynthesis.

chloroplast The organelle in plant and algal cells where photosynthesis takes place.

consumers Heterotrophs, which must eat or absorb organic food molecules because they are incapable of producing them.

energy The ability to do work.

food Organic (carbon-containing) molecules which store energy in the chemical bonds between their atoms.

food chain A pathway which traces energy flow from producers through consumers.

glucose The carbohydrate product of photosynthesis; serves as the universal fuel for life.

heat Thermal energy, the energy of vibrations in molecules – the "lowest" form of energy, which cannot easily be used for useful work.

heterotrophs Organisms which must consume organic molecules because they are incapable of synthesizing the food, or stored chemical energy, they need to work.

inorganic molecules Molecules which do not contain carbon (with a few exceptions such as carbon dioxide) and are not necessarily made by living organisms.

NADPH An energy carrier molecule produced in the light reactions of photosynthesis and used to build sugar in the Calvin cycle.

organic molecule A molecule which contains carbon, made by living organisms; examples include carbohydrates, lipids, and proteins.

photosynthesis The process by which plants, algae, and some bacteria transform sunlight into chemical energy and use it to produce carbohydrate food and oxygen for almost all life.

producer An autotroph, capable of synthesizing food molecules; forms basis of food chains.

Points to Consider

- Why do some people describe photosynthesis by plants as “making food from thin air”?
- Before we conclude this analysis of “the most important chemical reaction for life on Earth,” solidify your understanding of its importance by returning to the pizza, campfires, dolphins, automobiles, and glaciers. Can you connect them all to the chemical equation for photosynthesis (**Figure** 4.4)?
- You’ll be able to make more connections after studying the next chapter on cellular respiration. Can you already connect carbon dioxide and oxygen to automobiles?

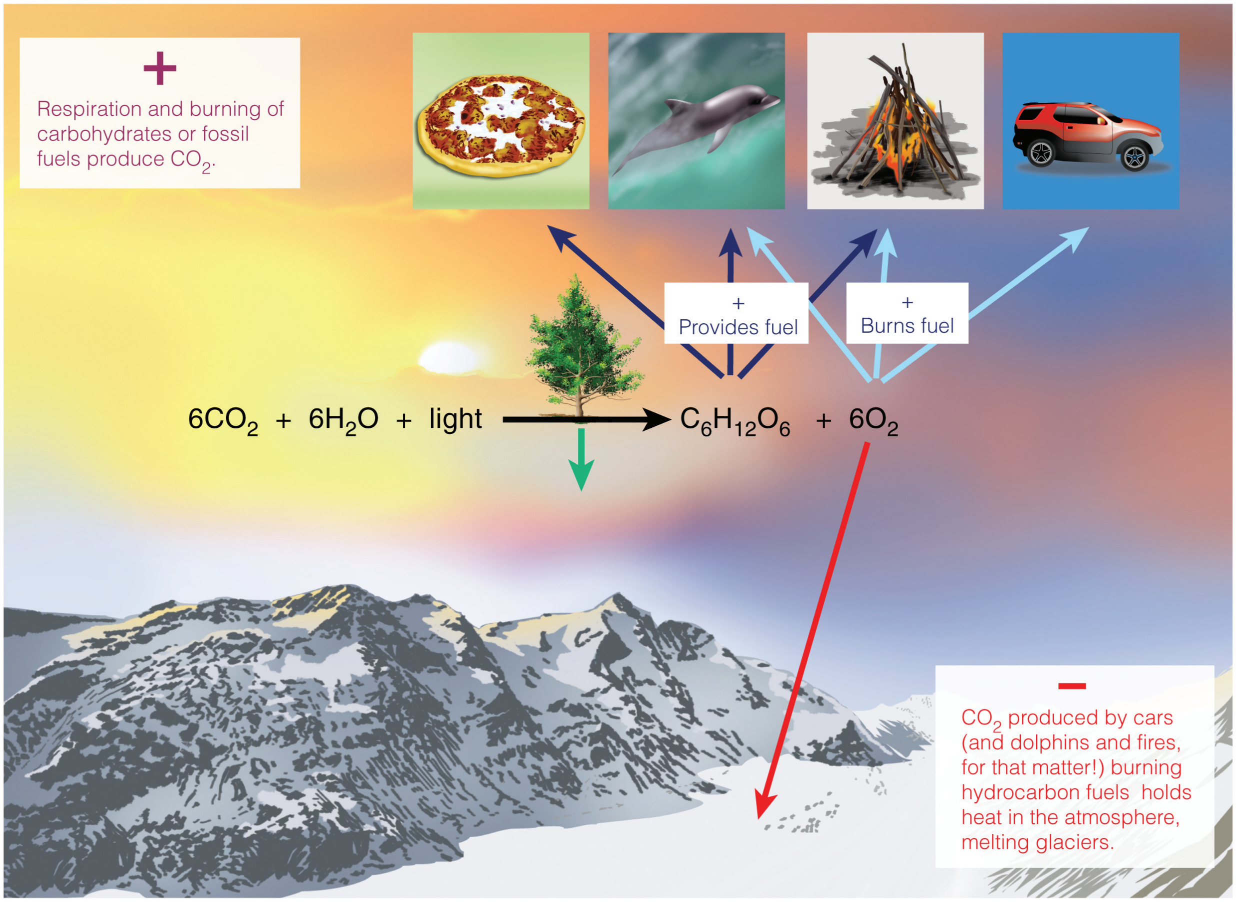

+
Respiration and burning of carbohydrates or fossil fuels produce CO_2.
$6CO_2 + 6H_2O + light \rightarrow C_6H_{12}O_6 + 6O_2$
+
Provides fuel
+
Burns fuel
–
CO_2 produced by cars (and dolphins and fires, for that matter!) burning hydrocarbon fuels holds heat in the atmosphere, melting glaciers.

Figure 4.4: (2)

4.2 Lesson 4.2: Into the Chloroplast: How Photosynthesis Works

Lesson Objectives

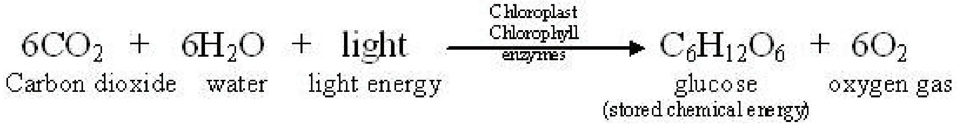
- Understand that hundreds of years of scientific exploration have contributed to our understanding of photosynthesis.
- Explain the contributions of Van Helmont, Priestley, and Melvin Calvin to our understanding of photosynthesis.
- Describe the structure and function of chloroplasts, thylakoids, and pigments.
- Explain how electron carrier molecules form electron transport chains.
- Trace the flow of energy and materials through the Light Reactions, including chemiosmosis.
- Trace the flow of energy and materials through The Calvin Cycle.
- Compare and contrast C-3, C-4, and CAM pathways for carbon fixation.

Introduction

Life requires photosynthesis for fuel and for the oxygen to burn that fuel. Since the Industrial Revolution (late 18th and early 19th centuries), we humans have relied on products of ancient photosynthesis for enormous quantities of fossil fuel energy. And, knowingly or not, we have also benefited from photosynthesis to remove the carbon dioxide produced when we burn those fuels. So it may not surprise you that biologists have studied this critical process in great detail. The goals of this lesson are:

- to discuss how scientists have explored this most important chemical reaction for life on earth
- to encourage you to appreciate just a little of its intricate beauty, and
- to understand how your own decisions and actions can influence the process of photosynthesis.

You've learned that a single chemical reaction represents the overall process of photosynthesis as demonstrated in the equation below.



$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{water}}{6H_2O} + \underset{\text{light energy}}{\text{light}} \xrightarrow{\substack{\text{Chloroplast}\\ \text{Chlorophyll}\\ \text{enzymes}}} \underset{\substack{\text{glucose}\\ \text{(stored chemical energy)}}}{C_6H_{12}O_6} + \underset{\text{oxygen gas}}{6O_2}$$

Although photosynthesis may seem straightforward in this form, such simplicity is deceiving for two reasons. First, the equation above summarizes dozens of individual chemical reactions involving many intermediate compounds. And second, just discovering major players like CO_2 and O_2 was challenging, because our ordinary senses cannot detect these molecules in "thin air!"

How do we know that the chemical reaction in photosynthesis really happens? Two famous historical experiments help us begin to understand this process.

Figure 4.5: In the 17th century, Jan Van Helmont, a Flemish chemist, physiologist, and physician, weighed and potted a willow tree, showing that plants do not get food from the soil. (15)

In the 17th century, people who thought about it at all assumed that plants get their food from the soil. Many people, encouraged by sellers of "plant food," still do. In 1638, Jan Baptist Van Helmont planted a 5 pound willow tree, like the one shown in **Figure** 4.5, in a 200 pound tub of soil. After 5 years of watering the plant, he weighed both again. The willow had gained over 160 pounds, but the soil had lost only 2 ounces. Van Helmont concluded that plants do not get their materials from soil, and inferred that they grow using materials from water (which he did not measure). As you know now, he was half right. Although soil provides important nutrients to plants, it supplies neither the energy nor the vast majority of the materials to build the plant. We must excuse him, because no one in the 17th century knew that carbon atoms form the basis of life, or that they float around in air in the form of carbon dioxide.

In the late 1770s, minister and natural philosopher Joseph Priestley burned a candle in a jar of air and observed that the candle burned out long before it ran out of wax. A similar experiment with a mouse resulted in the mouse's death. Priestley suggested that animals, like candles, "injure" the air. Adding a mint plant, as shown in **Figure** 4.6, however, "restored" the air which had been "injured" by the mouse or the candle. Only later, after many chemistry experiments, did Priestley publish his discovery of "dephlogisticated air." But in his studies of mice, plants, and candles, he had shown that plants produce, and animals consume, oxygen gas.

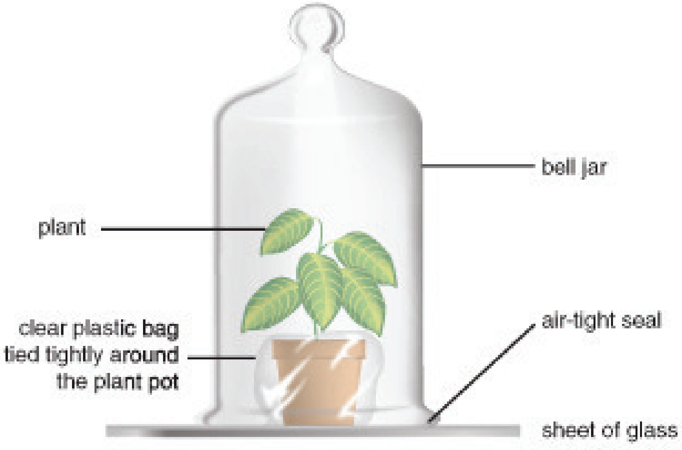


Figure 4.6: Joseph Priestly's bell jar experiment. (8)

During the 20th century, we learned that photosynthesis involves much more than just the three reactants, the three necessary conditions, and the two products shown in the equation. Using powerful microscopes, we've narrowed the process to one type of organelle within the plant – the chloroplast. In the next section, you will learn in more detail just how plants, algae, and photosynthetic bacteria make food for us all "from thin air." First, let's look at the organelle in which the drama of photosynthesis takes place and meet some of the key actors.

For a detailed animation of the complete photosynthesis process, see `http://vcell.ndsu.edu/animations/photosynthesis/first.htm.`

Chloroplasts: Theaters for Photosynthesis

If you examine a single leaf of the aquatic plant *Elodea*, shown in **Figure** 4.7, under a microscope, you will see within each cell dozens of small green ovals. These are **chloroplasts**, the organelles which conduct photosynthesis in plants and algae. Chloroplasts closely resemble some types of bacteria and even contain their own circular DNA and ribosomes. In fact, the **endosymbiotic theory** holds that chloroplasts were once independently living bacteria (prokaryotes). So when we say that photosynthesis occurs within chloroplasts, we speak not only of the organelles within plants and algae, but also of some bacteria – in other words, virtually all photosynthetic autotrophs.

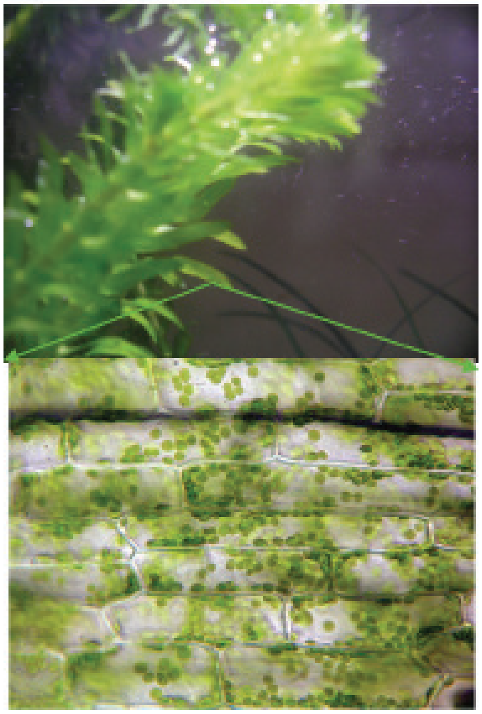


Figure 4.7: *Elodea* (above), like all plants and algae, consists of cells which contain organelles called chloroplasts (green ovals in the microphotograph below). If you look carefully at living cells through a microscope, you may see the chloroplasts moving slowly around the cell edges. The plant itself may not move, but this cyclosis hints at all the action within plant cells. (7)

Both chloroplasts and photosynthetic bacteria contain neat stacks (**grana**) of flattened sac-shaped membrane compartments (**thylakoids**), made in turn of elaborate and highly organized patterns of molecules which conduct photosynthesis, as shown in **Figure** 4.8. In addition to enzymes, two basic types of molecules - **pigments** and **electron carriers** – are key players.

Pigment molecules, often arranged together with proteins in large, complex **photosystems**, absorb specific wavelengths of light energy and reflect others; therefore, they appear colored. The most common photosynthetic pigment is **chlorophyll**, which absorbs blue-violet and red wavelengths of light, and reflects green (**Figure** 4.9 and **Figure** 4.10). **Accessory pigments** absorb other colors of light and then transfer the energy to chlorophyll. These include xanthophylls (yellow) and carotenoids (orange).

Electron carrier molecules are usually arranged in **electron transport chains** (ETCs). These accept and pass along energy-carrying electrons in small steps (**Figure** 4.11). In this way, they produce ATP and NADPH, which temporarily store chemical energy. Electrons

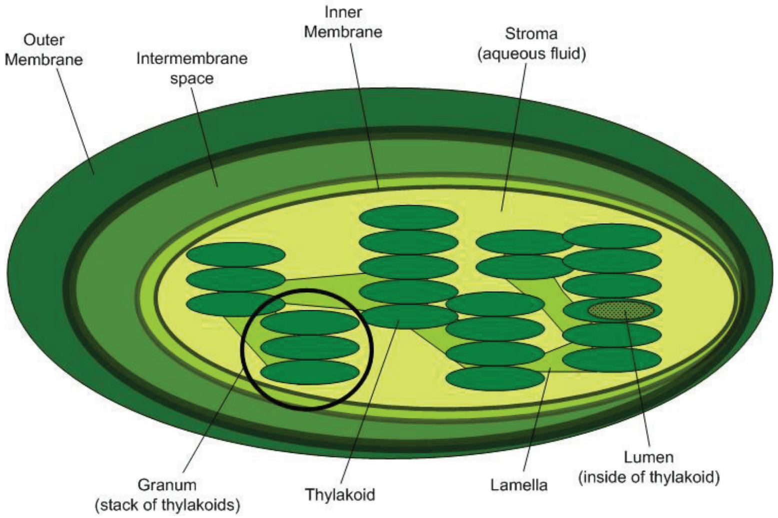


Figure 4.8: The structure of a chloroplast shows how membrane and molecular architecture helps life processes. Stacks of oval compartments (thylakoids) arrange chlorophyll, accessory pigment molecules, and photosynthetic proteins to capture sunlight and allow a concentration of ions within the sacs. You can see the green color of the chlorophyll. You cannot see the electron carriers, sequenced within the sac membranes, but their arrangement helps harvest small amounts of energy from excited electrons. (11)

in transport chains behave much like a ball bouncing down a set of stairs – a little energy is lost with each bounce. However, the energy "lost" at each step in an electron transport chain accomplishes a little bit of work, which eventually results in the synthesis of ATP.

Now that you've met some of the key players and explored the theater, let's put them together to see how the process unfolds. We will divide the process into two basic sets of reactions, known as the light reactions and the Calvin cycle, which uses carbon dioxide. As you study the details, refer frequently to the chemical equation of photosynthesis. In the first stage, you'll discover how chloroplasts transform light energy, and why we owe our ability to breathe to plants!

Photosynthesis Stage I: The Light Reactions: in which Chloroplasts Capture Sunlight Chemical Energy...

Every second, the sun fuses over 600 million tons of hydrogen into 596 tons of helium, converting over 4 tons of helium (4.3 billion kg) into light and heat energy. Countless tiny packets of that light energy travel 93 million miles (150 million km) through space, and about 1% of the light which reaches the Earth's surface participates in photosynthesis. Light is the source of energy for photosynthesis, and the first set of reactions which begin the process requires light – thus the name, Light Reactions, or Light-dependent Reactions.

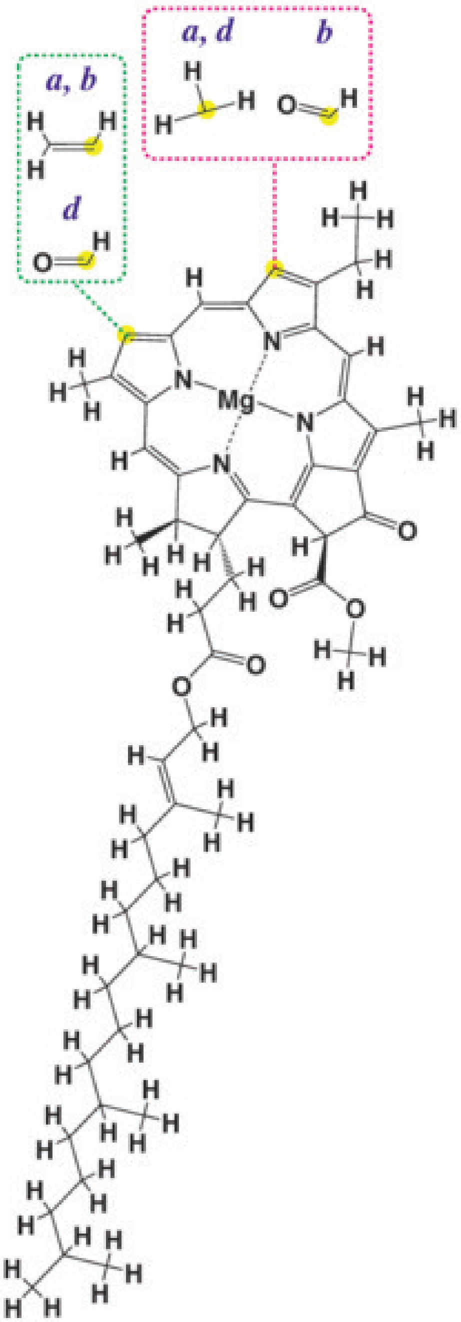


Figure 4.9: The pigment molecule, chlorophyll, appears green because its electrons absorb blue-violet and red light and reflect green, orange, and yellow light. This diagram shows that there are actually several different kinds of chlorophyll (a,b, and d shown here) in plants. (5)

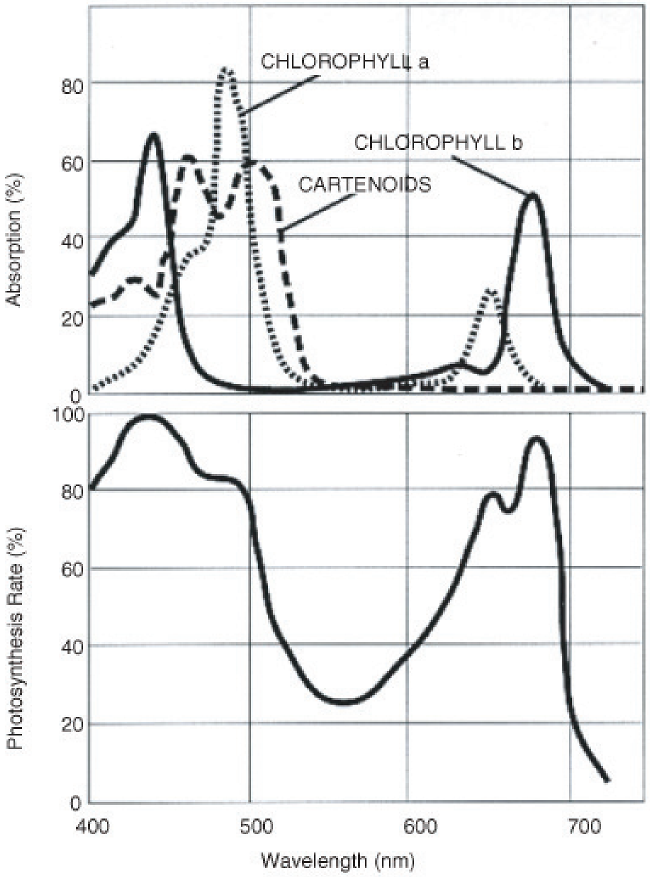


Figure 4.10: Each kind of pigment absorbs specific wavelengths (colors) of light. Sunlight contains many different wavelengths, which you see when they separate into a rainbow. Not all colors of light are used to make food for life. Most plants, algae, and photosynthetic bacteria appear green because they reflect green wavelengths. Their pigments have absorbed the violet-blue and red wavelengths. The amount of photosynthesis depends on the wavelength of light available. (16)

When light strikes chlorophyll (or an accessory pigment) within the chloroplast, it energizes electrons within that molecule. These electrons jump up to higher energy levels; they have absorbed or captured, and now carry, that energy. High-energy electrons are "excited." Who wouldn't be excited to hold the energy for life?

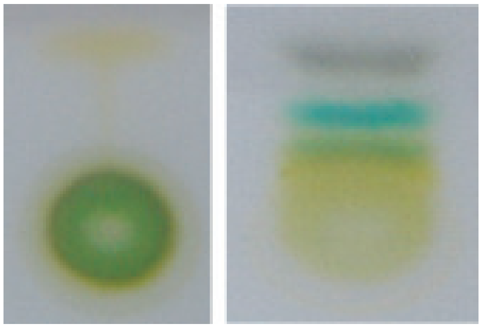


Figure 4.11: If you transfer spinach tissue onto a strip of paper and allow solvent to climb the paper, you can separate the pigment molecules. This technique for seeing molecules is known as chromatography ("color-writing"). The basic concept has many different applications in biochemistry. The images show two stages of a single chromatogram of spinach pigments. (1)

...And Change the Rules of Chemistry for Life!

The excited electrons leave chlorophyll to participate in further reactions, leaving the chlorophyll "at a loss"; eventually they must be replaced. That replacement process also requires light, working with an enzyme complex to split water molecules. In this process of **photolysis** ("splitting by light"), H_2O molecules are broken into hydrogen ions, electrons, and oxygen atoms. The electrons replace those originally lost from chlorophyll. Hydrogen ions and the high-energy electrons from chlorophyll will carry on the energy transformation drama after the Light Reactions are over.

The oxygen atoms, however, form oxygen gas, which is a waste product of photosynthesis (**Figure** 4.12). The oxygen given off supplies most of the oxygen in our atmosphere. Before photosynthesis evolved, Earth's atmosphere lacked oxygen altogether, and this highly reactive gas was toxic to the many organisms living at the time. Something had to change! Most contemporary organisms rely on oxygen for efficient respiration. So plants don't just "restore" the air, as Priestley suggested. They also had a major role in creating it!

To summarize, chloroplasts "capture" sunlight energy in two ways. Light "excites" electrons in pigment molecules, and light provides the energy to split water molecules, providing more electrons as well as hydrogen ions.

Now let's follow those excited electrons...

Nitrogen	78.084%
Oxygen	20.946%
Argon	0.934%
Carbon dioxide	0.038%
Water vapor	1%
Other	0.002%

Figure 4.12: Photosynthesis has made the Earth's atmosphere today very different from what it was 2-3 billion years ago, by giving off oxygen gas as waste. The table to the right shows the composition of today's atmosphere. On the left is an Apollo 17 photograph of Earth. (12)

How Do Chloroplasts Convert Light Energy to Chemical Energy?

Excited electrons which have absorbed light energy are unstable. However, the highly organized **electron carrier** molecules embedded in chloroplast membranes order the flow of these electrons, directing them through electron transport chains (ETCs). At each transfer, small amounts of energy released by the electrons are captured and put to work or stored. Some is also lost as heat with each transfer, but overall the light reactions are extremely efficient at capturing light energy and transforming it to chemical energy.

Two sequential transport chains harvest the energy of excited electrons, as shown in **Figure** 4.13.

(1) First, they pass down an ETC which captures their energy and uses it to pump hydrogen ions by active transport into the thylakoids. These concentrated ions store potential energy by forming a **chemiosmotic** or **electrochemical gradient** – a higher concentration of both positive charge and hydrogen inside the thylakoid than outside. (The gradient formed by the H^+ ions is known as a chemiosmotic gradient.) Picture this energy buildup of H^+ as a dam holding back a waterfall. Like water flowing through a hole in the dam, hydrogen ions "slide down" their concentration gradient through a membrane protein which acts as both ion channel and enzyme. As they flow, the ion channel/enzyme **ATP synthase** uses their energy to chemically bond a phosphate group to ADP, making ATP.

(2) Light re-energizes the electrons, and they travel down a second electron transport chain (ETC), eventually bonding hydrogen ions to $NADP^+$ to form a more stable energy storage molecule, NADPH. NADPH is sometimes called "hot hydrogen," and its energy and hydrogen atoms will be used to help build sugar in the second stage of

photosynthesis.

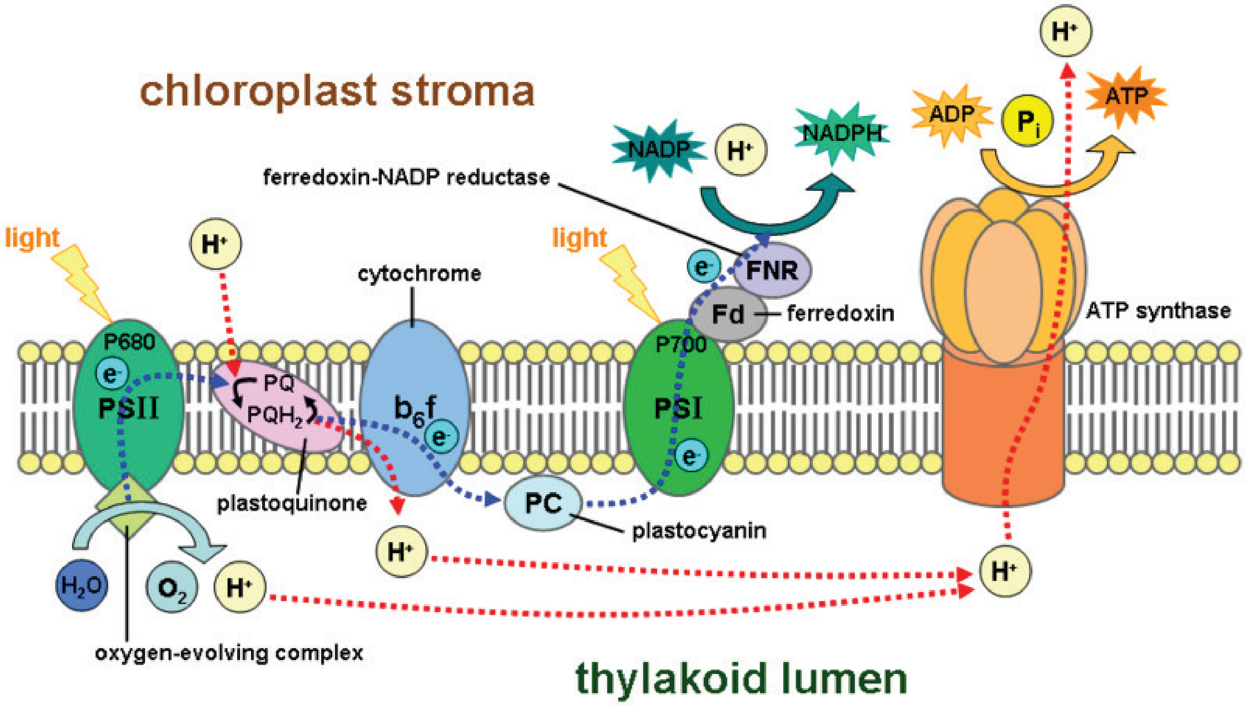


Figure 4.13: Membrane architecture: The large colored carrier molecules form electron transport chains which capture small amounts of energy from excited electrons in order to store it in ATP and NADPH. Follow the energy pathways: light ⟶ electrons ⟶ NADPH (blue line) and light ⟶ electrons ⟶ concentrated H^+ ⟶ ATP (red line). Note the intricate organization of the chloroplast. (10)

NADPH and ATP molecules now store the energy from excited electrons – energy which was originally sunlight – in chemical bonds. Thus chloroplasts, with their orderly arrangement of pigments, enzymes, and electron transport chains, transform light energy into chemical energy. The first stage of photosynthesis – **light-dependent reactions** or simply "light reactions" – is complete.

Photosynthesis Stage II: The Calvin Cycle - Making Food "From Thin Air"

You've learned that the first, light-dependent stage of photosynthesis uses two of the three reactants - water and light - and produces one of the products - oxygen gas (a waste product of this process). All three necessary conditions are required – chlorophyll pigments, the chloroplast "theater," and enzyme catalysts. The first stage transforms light energy into chemical energy, stored to this point in molecules of ATP and NADPH. Look again at the overall equation below. What is left?

$$\underset{\text{Carbon dioxide}}{6CO_2} + \underset{\text{water}}{6H_2O} + \underset{\text{light energy}}{\text{light}} \longrightarrow \underset{\substack{\text{glucose} \\ \text{(stored chemical energy)}}}{C_6H_{12}O_6} + \underset{\text{oxygen gas}}{6O_2}$$

Waiting in the wings is one more reactant – carbon dioxide, and yet to come is the star product which is food for all life – glucose. These key players perform in the second act of the photosynthesis drama, in which food is “made from thin air!”

The second stage of photosynthesis can proceed without light, so its steps are sometimes called “light-independent” or “dark” reactions. Many biologists honor the scientist, Melvin Calvin, who won a 1961 Nobel Prize for working out this complex set of chemical reactions, naming it the Calvin Cycle.

The Calvin Cycle has two parts. First carbon dioxide is ”fixed.” Then ATP and NADPH from the Light Reactions provide energy to combine the fixed carbons to make sugar.

Carbon Dioxide is “Fixed”

Why does carbon dioxide need to be fixed? Was it ever broken?

Life on Earth is carbon-based. Organisms need not only energy but also carbon atoms for building bodies. For nearly all life, the ultimate source of carbon is carbon dioxide (CO_2), an **inorganic molecule**. CO_2, as you saw in **Figure** 4.14, **makes up .038% of the Earth’s atmosphere.**

Animals and most other heterotrophs cannot take in CO_2 directly. They must eat other organisms or absorb **organic molecules** to get carbon. Only autotrophs can build low-energy inorganic CO_2 into high-energy **organic molecules** like glucose. This process is **carbon fixation**.

Plants have evolved three pathways for carbon fixation.

The most common pathway combines one molecule of CO_2 with a 5-carbon sugar called ribulose biphosphate (RuBP). The enzyme which catalyzes this reaction (nicknamed **RuBisCo**) is the most abundant enzyme on earth! The resulting 6-carbon molecule is unstable, so it immediately splits into two 3-carbon molecules. The 3 carbons in the first stable molecule of this pathway give this largest group of plants the name “C-3.”

Dry air, hot temperatures, and bright sunlight slow the C-3 pathway for carbon fixation. This is because **stomata**, tiny openings under the leaf which normally allow CO_2 to enter and O_2 to leave, must close to prevent loss of water vapor (**Figure** 4.14). Closed stomata lead to a shortage of CO_2. Two alternative pathways for carbon fixation demonstrate biochemical adaptations to differing environments.

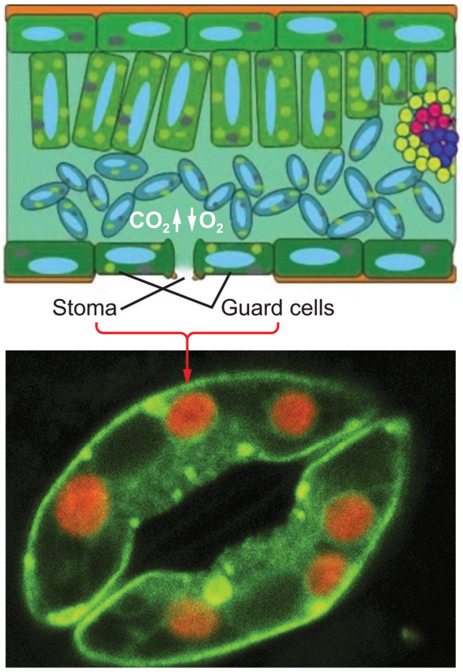


Figure 4.14: Stomata on the underside of leaves take in CO_2 and release water and O_2. Guard cells close the stomata when water is scarce. Leaf cross-section (above) and stoma (below). (3)

Plants such as corn solve the problem by using a separate compartment to fix CO_2. Here CO_2 combines with a 3-carbon molecule, resulting in a 4-carbon molecule. Because the first stable organic molecule has four carbons, this adaptation has the name C-4. Shuttled away from the initial fixation site, the 4-carbon molecule is actually broken back down into CO_2, and when enough accumulates, Rubisco fixes it a second time! Compartmentalization allows efficient use of low concentrations of carbon dioxide in these specialized plants.

Cacti and succulents such as the jade plant avoid water loss by fixing CO_2 only at night. These plants close their stomata during the day and open them only in the cooler and more humid nighttime hours. Leaf structure differs slightly from that of C-4 plants, but the fixation pathways are similar. The family of plants in which this pathway was discovered gives the pathway its name, Crassulacean Acid Metabolism, or CAM (**Figure** 4.15). All three carbon fixation pathways lead to the Calvin Cycle to build sugar.

Figure 4.15: Even chemical reactions adapt to specific environments! Carbon fixation pathways vary among three groups. Temperate species (maple tree, left) use the C-3 pathway. C-4 species (corn, center) concentrate CO_2 in a separate compartment to lessen water loss in hot bright climates. Desert plants (jade plant, right) fix CO_2 only at night, closing stomata in the daytime to conserve water. (9)

How Does the Calvin Cycle Store Energy in Sugar?

As Melvin Calvin discovered, carbon fixation is the first step of a cycle. Like an electron transport chain, the Calvin cycle, shown in **Figure** 4.16, transfers energy in small, controlled steps. Each step pushes molecules uphill in terms of energy content. Recall that in the electron transfer chain, excited electrons lose energy to NADPH and ATP. In the Calvin Cycle, NADPH and ATP formed in the light reactions lose their stored chemical energy to build glucose.

Use the diagram below to identify the major aspects of the process:

- the general cycle pattern
- the major reactants

- the products

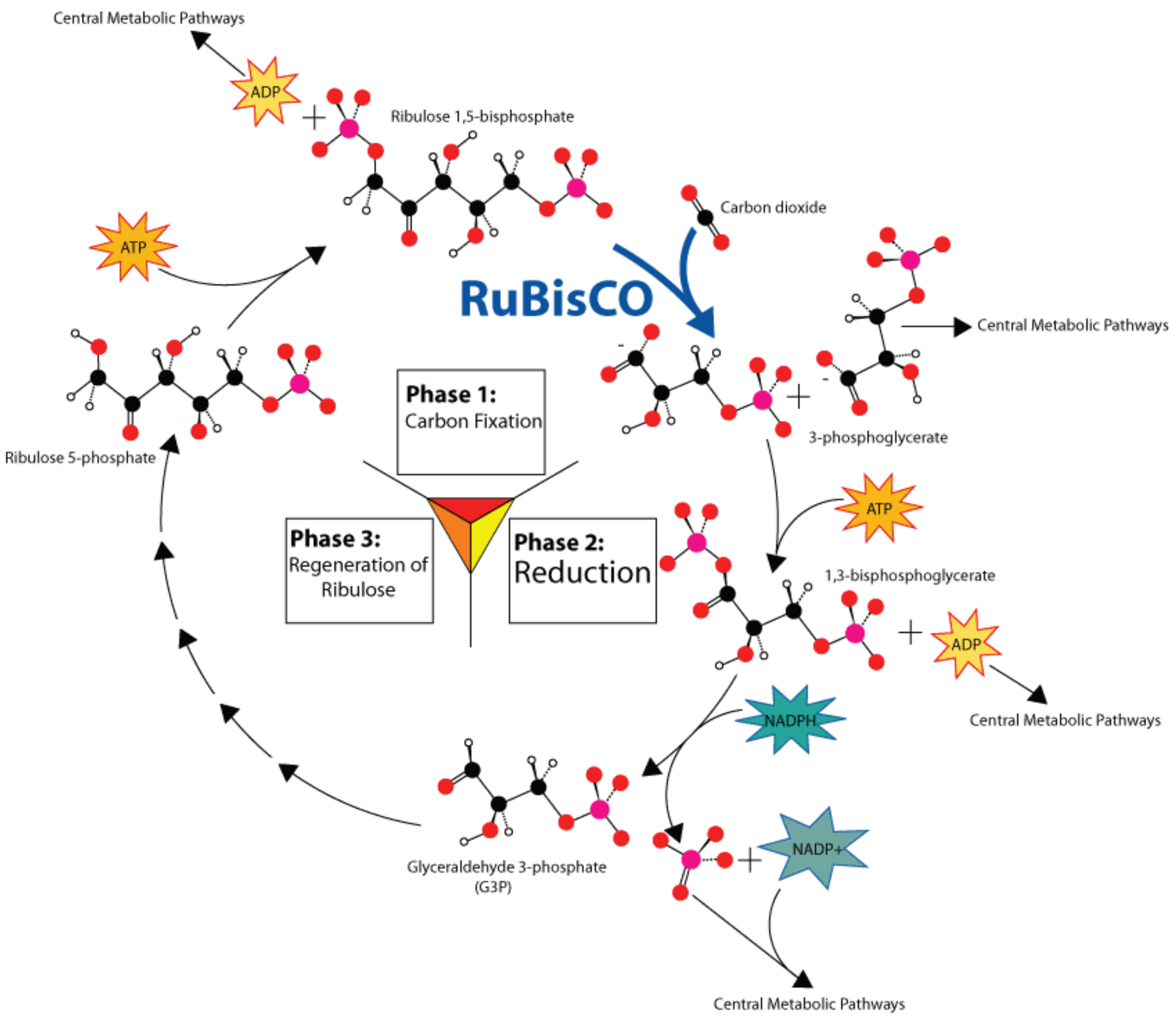


Figure 4.16: Overview of the Calvin Cycle Pathway. (13)

First, notice where carbon is fixed by the enzyme nicknamed Rubisco. In C-3, C-4, and CAM plants, CO_2 enters the cycle by joining with 5-carbon ribulose bisphosphate to form a 6-carbon intermediate, which splits (so quickly that it isn't even shown!) into two 3-carbon molecules.

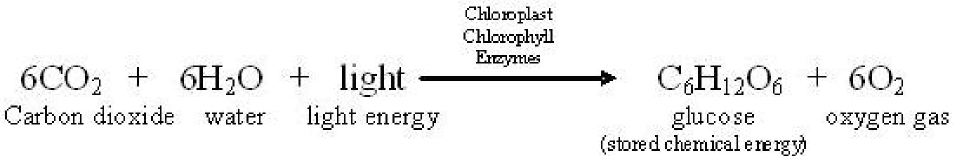
Now look for the points at which ATP and NADPH (made in the light reactions) add chemical energy ("Reduction" in the diagram) to the 3-carbon molecules. The resulting "half-sugars" can enter several different metabolic pathways. One recreates the original 5-carbon precursor, completing the cycle. A second combines two of the 3-carbon molecules to form glucose, universal fuel for life.

The cycle begins and ends with the same molecule, but the process combines carbon and energy to build carbohydrates – food for life.

So – how does photosynthesis store energy in sugar? Six "turns" of the Calvin cycle use chemical energy from ATP to combine six carbon atoms from six CO_2 molecules with 12 "hot hydrogens" from NADPH. The result is one molecule of glucose, $C_6H_{12}O_6$.

Lesson Summary

The single chemical equation below represents the overall process of photosynthesis as well as summarizes many individual chemical reactions that were understood only after hundreds of years of scientific exploration.



$$6CO_2 + 6H_2O + \text{light} \xrightarrow{\text{Chloroplast Chlorophyll Enzymes}} C_6H_{12}O_6 + 6O_2$$

Chloroplasts are the organelles where the process of photosynthesis takes place in plants and algae.

- Chloroplasts resemble blue green bacteria, containing their own DNA and ribosomes.
- The **Endosymbiotic Theory** holds that chloroplasts once were independent prokaryotic cells, but were engulfed by other larger prokaryotes, forming the first eukaryotic cells.
- Chloroplasts are made of membranes, which enclose stacks of membrane sacs called thylakoids.
- The membranes sequence **pigments** and **electron carrier molecules** for efficient photosynthesis.
- **Thylakoids** create compartments, which allow concentration gradients to store energy.
- **Pigment** molecules absorb specific wavelengths (colors) of light; chlorophyll is the primary pigment in photosynthesis.
- **Electron carrier molecules** form **electron transport chains**, which transfer energy in small steps so that the energy can be stored or used for work.

Photosynthesis consists of two groups of chemical reactions: the Light Reactions and the Calvin Cycle.

Light Reactions transform energy from sunlight into chemical energy, and produce and release oxygen gas.

- When light strikes pigment molecules, electrons absorb its energy and are excited.

- Light also provides energy to split water molecules into electrons, hydrogen ions, and oxygen gas.
- The oxygen gas is released as "waste", but it is the source of the oxygen in Earth's atmosphere.
- Two pathways capture the energy from excited electrons as chemical energy stored in the bonds of molecules; both pathways involve **electron transport chains**.
  - One produces **NADPH** molecules, which stores energy and "hot hydrogen".
  - A second pumps hydrogen ions into the thylakoids, forming an electrochemical gradient whose energy builds **ATP** molecules. This is "chemiosmosis".

The Calvin Cycle uses the NADPH and ATP from the Light Reactions to "fix" carbon and produce glucose.

- Stomata underneath plant leaves allow gases (CO_2, H_2O, and O_2) to enter and exit the leaf interior.
- Carbon dioxide enters the Calvin Cycle when an enzyme nicknamed "Rubisco" attaches it to a 5-carbon sugar. The unstable 6-carbon compound immediately breaks into two 3-carbon compounds, which continue the cycle.
- Most plants fix CO_2 directly with this pathway, so they are called C-3 plants.
- Some plants have evolved preliminary fixation pathways, which help them conserve water in hot, dry habitats, but eventually the carbon enters the cycle along the "Rubisco" pathway.
  - C-4 plants such as corn use a 3-carbon carrier to compartmentalize initial carbon fixation in order to concentrate CO_2 before sending it on to Rubisco.
  - CAM plants such as jade plants and some cacti open their stomata for preliminary CO_2 fixation only at night.
- In the Calvin Cycle, the fixed CO_2 moves through a series of chemical reactions, gaining a small amount of energy (or "hot hydrogens") from ATP or NADPH at each step.
- Six turns of the cycle process 6 molecules of carbon dioxide and 12 "hot hydrogens" to produce a single molecule of glucose.
- The cycle begins and ends with the same 5-carbon molecule, but the process stores chemical energy in food for nearly all life.

Summary Animations

- These interactive web sites depicts each step of photosynthesis in great detail.

http://www.johnkyrk.com/photosynthesis.html
http://www.johnkyrk.com/photosynthesisdark.html

Review Questions

1. Summarize Jan Van Helmont's willow tree experiment. State his conclusion and the inference he made after his experiment, and explain how his data supports each. Finally, relate his findings to what we know today about the overall process of photosynthesis.
2. Using the overall equation for photosynthesis, explain which components relate to J.B. Priestley's observation that "Plants restore the air that animals injure."
3. Explain how the structure of a chloroplast – its membranes and thylakoids – makes its function – the chemical reactions of photosynthesis – more efficient.
4. Summarize the Endosymbiotic Theory. What evidence related to chloroplasts supports this theory?
5. Name the two stages (sets of reactions) which make up the process of photosynthesis.
6. Match the major events with the stage of photosynthesis in which they occur. **Stages**Light Reactions
   Calvin Cycle
   Major Events

   (a) Carbon dioxide is fixed.
   (b) Electrons in chlorophyll jump to higher energy levels.
   (c) Glucose is produced.
   (d) NADPH and ATP are produced.
   (e) NADPH and ATP are used.
   (f) Oxygen gas is released.
   (g) Water is split.

7. Use your understanding of pigments to explain why the living world appears green. Then think a little further and offer a hypothesis to explain why the world is not black!
8. Explain the value of cycles of chemical reactions, such as the Calvin Cycle.
9. Explain how their various methods of carbon fixation adapt C-3, C-4, and CAM plants to different habitats.
10. We humans depend on photosynthesis, and our actions in turn affect photosynthesis. Explain how humans depend on photosynthesis for:

    (a) food
    (b) building materials for furniture and homes
    (c) fuel for vehicles, heat, and electricity
    (d) breathable air

    Explain how the following actions would affect photosynthesis:

    (a) We may clear-cut a forest for timber and parking lot space
    (b) When we burn fossil fuels for transportation or heat, we release CO2 into the atmosphere
    (c) When we dam up and overuse water in a certain area, the area water table drops

Further Reading / Supplemental Links

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- `http://vcell.ndsu.nodak.edu/animations/photosynthesis/index.htm.`

Vocabulary

accessory pigment A molecule which absorbs colors of light other than blue-violet and red, and then transfers the energy to chlorophyll.

ATP synthase Ion channel and enzyme complex that chemically bonds a phosphate group to ADP, making ATP as H^+ ions flow through the ion channel.

Calvin Cycle The second stage of photosynthesis, which can proceed without light, so its steps are sometimes called "light-independent" or "dark" reactions; results in the formation of a sugar.

carbon fixation The process which converts carbon dioxide in the air to organic molecules, as in photosynthesis.

chlorophyll The primary pigment of photosynthesis.

chloroplast The organelle in plant and algal cells where photosynthesis takes place.

electron carrier A molecule which transfers energy-carrying electrons within an electron transport chain.

electron transport chain (ETC) A series of electron-carrying molecules which accept and pass along energy-carrying electrons in small steps, allowing the energy lost at each transfer to be captured for storage or work.

endosymbiotic theory The theory which states that chloroplasts and mitochondria originated as independent prokaryotic cells which were engulfed by larger prokaryotic cells to form the first eukaryotic cells.

glucose The carbohydrate product of photosynthesis; serves as the universal fuel for life.

light-dependent reactions The first set of reactions of photosynthesis; requires sunlight; also called the light reactions.

NADPH An energy carrier molecule produced in the light reactions of photosynthesis; used to build sugar in the Calvin cycle.

photolysis The light reaction process of splitting water molecules into electrons, hydrogen ions, and oxygen gas.

photosynthesis The process by which plants, algae, and some bacteria transform sunlight into chemical energy and use it to produce carbohydrate food and oxygen for almost all life.

photosystem A cluster of proteins and pigments found in chloroplasts and active in photosynthesis.

pigment A molecule which absorbs specific wavelengths of light energy and reflects others and therefore appears colored.

RuBisCo The enzyme that combines one molecule of CO_2 with a 5-carbon sugar called ribulose biphosphate (RuBP); the most abundant enzyme on earth.

stomata (singular stoma) Openings on the underside of a leaf which allow gas exchange and transpiration.

thylakoid Flattened sac-shaped compartment within a chloroplast, made of membranes embedded with molecules which carry out photosynthesis.

Points to Consider

- Recall Priestley's early observation that plants "restore the air." Name some ways that plants and algae affect the atmosphere.
- Which of your own activities affect photosynthesis? Think "globally" in addition to "locally" and add large-scale human activities to your list. Are there any changes you could make in your life which could promote photosynthesis and a healthy atmosphere?
- You learned in this chapter that plants make "food" which life needs for energy. But is it usable energy? Or does it need to be converted into some other type of energy? What do you think and why?

Image Sources

(1) *http://commons.wikimedia.org/wiki/File:Chromatography_of_chlorophyll_-_Step_6.jpg*. CC-BY-SA 2.5.

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